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Bt Corn and Insect Resistance: An Economic Assessment of Refuges

Terrance M. Hurley, Bruce A. Babcock, and Richard L. Hellmich

Genetically engineered crops offer farmers a new option for controlling pests. The high efficacy of these pesticidal crops, combined with the potential for widespread adoption, has raised concerns that pest resistance may prematurely diminish their value. In response to these concerns, the Environmental Protection Agency requires resistance management plans. Current resistance management plans rely on a high-dose refuge strategy. This analysis extends the current framework for evaluating high-dose refuge strategies to include a measure of agricultural productivity and conventional pesticide use. The economic tradeoff relative to agricultural productivity, conventional pesticide use, and pest resistance is assessed when Bt corn is planted to control the European corn borer.

Key words: biotechnology, corn, European corn borer, genetically modified organisms, high-dose refuge, resistance management, transgenic crops

Introduction

Proteins from the soil bacterium *Bacillus thuringiensis* (Bt) are toxic to a variety of insects. These naturally occurring pesticides have been used by organic farmers for decades. Scientists can now insert genes into crops to allow plants to produce Bt proteins that protect them against insects such as the cotton bollworm, Colorado potato beetle, and European corn borer (ECB).

Bt crops offer farmers a new tool for pest control, thus reducing their reliance on more hazardous conventional pesticides. Unfortunately, pests have demonstrated the ability to become resistant to Bt (Hama, Suzuki, and Tanaka; Tabashnik et al. 1992, 1995; Martinez-Ramirez et al.). Responding to resistance concerns, the Environmental Protection Agency (EPA) has taken an active role in encouraging the development of resistance management plans for Bt crops.

Past studies provide a rationale for the EPA's involvement. Since pests propagate and damage crops, they are a detrimental renewable resource (Hueth and Regev; Regev, Gutierrez, and Feder; Regev, Shalit, and Gutierrez). In addition, pest susceptibility (the converse of resistance) is a valuable nonrenewable resource since susceptible pests can

Terrance M. Hurley is assistant professor, Department of Applied Economics, University of Minnesota, St. Paul; Bruce A. Babcock is professor, Department of Economics, Iowa State University; and Richard L. Hellmich is research entomologist with the U.S. Department of Agriculture, Agricultural Research Service, Corn Insects and Crop Genetics Research Unit, Department of Entomology, Iowa State University. The authors gratefully acknowledge the useful comments of three anonymous referees and financial support provided by the Center for Agricultural and Rural Development, the Minnesota Agricultural Experiment Station, Monsanto Company, and AgrEvo USA.

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be controlled (Hueth and Regev; Regev, Shalit, and Gutierrez). Capturing this value, however, results in an increasingly resistant pest. The degree to which private pest control is optimal depends on pest mobility. Socially optimal control accounting for both the renewable and nonrenewable nature of pests and pest susceptibility results if pests are immobile because control decisions are internalized.[1] Deviations from socially optimal control result when a pest is mobile and treated as common property because there is no incentive for farmers to consider the effect of pest control decisions and decreasing susceptibility on neighbors.

Industry and academic scientists have argued for a high-dose refuge strategy to combat resistance to Bt crops. The foundations of this strategy are to have Bt crops express enough toxins to kill all but the most resistant pests and for farmers to plant a portion of their acreage to refuge where the Bt is not used for pest control. Refuges allow susceptible pests to thrive and mate with resistant pests, thereby reducing selection pressure and slowing the proliferation of resistance.

How much refuge should be planted is a key issue. Ostlie, Hutchison, and Hellmich recommend 20% to 30% refuge for Bt corn in the north central United States when refuge is not treated with conventional pesticides for supplemental control, and 40% if supplemental control is planned. In 1998, a scientific advisory panel convened by the EPA argued for enough refuge to provide 500 susceptible mates for each resistant pest (FIFRA Scientific Advisory Panel). Mellon and Rissler recommend 25% to 50% refuge depending on compliance and use of supplemental control. The International Life Science Institute/Health and Environmental Science Institute (ILSI/HESI) recommends 5% to 40% untreated and 10% to 80% treated refuge depending on the risk of resistance. Most recently, members of industry submitted a unified plan to the EPA (Demetra et al.) that proposed 20% refuge allowing for supplemental control using economic treatment thresholds. The EPA accepted this proposal for the 2000 growing season.

Bt crops provide benefits by increasing agricultural productivity and reducing the use of more hazardous conventional pesticides. While these benefits have not been completely ignored, they are generally not made explicit when evaluating refuge recommendations. The purpose of this investigation is to extend the current framework for evaluating refuge recommendations to include explicit measures of agricultural productivity and conventional pesticide use. The new framework is then applied to assess refuge recommendations for Bt corn in the north central United States.

Four results emerge from the analysis. First, planting refuge not only reduces resistance, but also benefits agricultural productivity in the long run because it preserves the efficacy of Bt. Second, the productivity benefits of resistance management as well as the costs are extremely sensitive to pest population dynamics. Third, while the average cost of increasing refuge to slow resistance is usually low, the marginal cost is often substantial. Fourth, more refuge is needed for resistance management when supplemental spray applications are economical and frequent on refuge.

The Conceptual Model

Consider a simplified production region with a single crop and pest (as outlined in Roush and Osmond; Gould; and Onstad and Gould 1998a, b). A closed pest population

[1] The socially optimal decision will result provided pest susceptibility is valued only for its pest control benefits and there are no external costs attributable to the Bt toxin.

with negligible migration defines the size of the region. While a single crop is planted, there are two varieties.[2] The first, denoted by $i = 0$, is a refuge crop with normal pest survival rates. The second, denoted by $i = 1$, is a Bt crop with lower than normal pest survival rates. The proportion of refuge planted each season is $1.0 \geq \phi \geq 0.0$.[3] The $1 \times G$ vector (τ) denotes the set of economic treatment thresholds used to trigger supplemental conventional pesticide treatments, where G is the number of generations of pests in a season.[4] The expected pest-free yield and real price for the ith crop are Y^i and P^i, respectively. The proportion of resistance and level of pest pressure at the beginning of season t are $1.0 \geq R_t \geq 0$, and $N_t \geq 0.0$. The proportion of yield loss and production cost for the ith crop in season t are $1.0 \geq D_t^i \geq 0.0$, and $C_t^i \geq 0.0$.

The evolution of resistance depends on refuge, treatment thresholds, and current pest pressure and resistance:

$$(1) \qquad R_{t+1} = r(R_t, N_t, \phi, \tau).$$

Characterizing pest susceptibility as a nonrenewable resource implies resistance will never decrease. Thus, R_{t+1} is nondecreasing in R_t. Increasing refuge would seem to increase the proportion of susceptible mates and decrease resistance. However, increasing refuge also increases pest pressure since fewer pests are exposed to Bt, which can result in supplemental treatments later in the season, particularly on unprotected refuge. A supplemental treatment on refuge but not Bt acreage exacerbates resistance because fewer susceptible pests survive to mate. If supplemental treatments on refuge are triggered, R_{t+1} can increase in ϕ; otherwise, R_{t+1} tends to decrease in ϕ. When current pest pressure is high or treatment thresholds low, supplemental treatments are more likely, such that R_{t+1} increases as N_t increases and as τ decreases.

The evolution of pest pressure also depends on refuge, treatment thresholds, and current pest pressure and resistance, but in more complex ways:

$$(2) \qquad N_{t+1} = n(N_t, R_t, \phi, \tau).$$

Surviving pests propagate but also compete for resources such as food. Supplemental treatments are warranted when pest pressure is high. Therefore, N_{t+1} tends to increase in N_t when populations are low because resources are abundant and supplemental treatments unwarranted. Also, N_{t+1} tends to decrease when populations are high because resources are scarce and supplemental treatments warranted. As resistance increases, so do pest survival rates, which can trigger supplemental treatments. Therefore, N_{t+1} tends to increase in R_t when survival rates do not warrant supplemental treatments. If survival rates are high enough for supplemental treatments, N_{t+1} may be increasing or decreasing in R_t.

Increasing refuge has three effects. Refuge increases pest survival rates since fewer pests are exposed to Bt. With higher survival rates, supplemental treatments may be warranted. Refuge also lowers survival rates later in the season by slowing resistance.

[2] Current EPA guidelines require the refuge crop to be the same as the Bt crop.

[3] Results of earlier studies (Hueth and Regev; and Regev, Shalit, and Gutierrez) suggest that the optimal management of resistance using refuge will require temporal adjustments. However, to maintain comparability with the current framework and a more manageable scope, we forego these temporal adjustments and focus on a second-best solution with a constant proportion of refuge in every season.

[4] Many pests complete multiple generations in a season. Since each generation appears at different stages of crop development, economic treatment thresholds typically differ by generation.

Therefore, N_{t+1} may be increasing or decreasing in ϕ regardless of whether supplemental treatments are warranted. N_{t+1} may be increasing or decreasing in τ because while more pests appear to be controlled, more resistance increases survival rates later in the season.

Pest pressure throughout the season determines yield loss and depends on refuge, treatment thresholds, and current pest pressure and resistance:

$$D_t^i = d^i(N_t, R_t, \phi, \tau). \tag{3}$$

When current pest pressure or resistance is high, more pests survive unless supplemental treatments are triggered. With supplemental treatments, the survival rate can be lower. Therefore, D_t^i may be increasing or decreasing in N_t and R_t. Increasing refuge slows resistance throughout the season, but also decreases pest exposure to Bt, increasing the need for supplemental treatments later in the season; therefore, D_t^i may be increasing or decreasing in ϕ. Decreasing treatment thresholds decrease pest pressure and damages, but can also exacerbate resistance. Later in the season, an increase in resistance can raise survival rates and increase yield loss, such that D_t^i may be increasing or decreasing in τ.

There are two components to the production cost. C^i is the per acre cost of items such as labor, machinery, fertilizer, herbicides, seed, and scouting that do not depend on supplemental treatments. A $1 \times G$ vector ($\mathbf{c}^i$) is the per acre pesticide and application cost of supplemental treatments by generation. The $1 \times G$ vector, $\eta^i(N_t, R_t, \phi, \tau)$, has elements equal to 1.0 for generations with supplemental treatments, and 0.0 otherwise. Due to the complex interaction among refuge, treatment thresholds, and current pest pressure and resistance, the effects of N_t, R_t, ϕ, and τ on $\eta^i(N_t, R_t, \phi, \tau)$, are generally ambiguous. The per acre cost of production for the ith crop in season t is specified as:

$$C_t^i = C^i + \mathbf{c}^i \cdot \eta^i(N_t, R_t, \phi, \tau). \tag{4}$$

A richer assessment of the economic and environmental tradeoffs of refuge is obtained by exploring the effect of refuge on agricultural productivity, conventional pesticide use, and resistance. Agricultural productivity is measured using the average per acre annualized net present value of production over T seasons:

$$\Pi(\phi) = \sum_{t=0}^{T-1} \delta^t \pi_t(\phi) \Big/ \sum_{t=0}^{T-1} \delta^t, \tag{5}$$

where δ is the discount rate, and

$$\pi_t(\phi) = \phi\left\{P^0 Y^0(1 - D_t^0) - C_t^0\right\} + (1 - \phi)\left\{P^1 Y^1(1 - D_t^1) - C_t^1\right\}$$

is the average of per acre revenues minus production cost for the refuge and Bt acreage during season t weighted by the proportion of refuge planted.

Conventional pesticide use is measured using the annual frequency of applications in T seasons:

$$\gamma(\phi) = \sum_{t=0}^{T-1} \mathbf{I}_G \cdot \left[\phi\eta^0(N_t, R_t, \phi, \tau) + (1 - \phi)\eta^1(N_t, R_t, \phi, \tau)\right] \Big/ T, \tag{6}$$

where $\mathbf{I}_G$ is a $1 \times G$ identity vector. Resistance is measured using the final level of resistance at the end of T seasons, R_T.

The objective is to find the proportion of refuge that maximizes agricultural productivity, while maintaining conventional pesticide use and resistance below politically or ecologically acceptable thresholds. This constrained optimization is subject to equations (1)–(4), $1.0 \geq \phi \geq 0.0$, initial pest pressure N_0, and initial resistance R_0. The Lagrangian is:

$$L = \Pi(\phi) + \lambda_\Gamma(\Gamma - \gamma(\phi)) + \lambda_\Omega(\Omega - R_t), \tag{7}$$

where Γ and Ω are the maximum acceptable levels of pesticide use and resistance, respectively, and λ_Γ and λ_Ω are the corresponding Lagrangian multipliers.

The first-order marginal condition for an interior solution is specified as:

$$\frac{\partial \Pi(\phi)}{\partial \phi} = \lambda_\Gamma \frac{\partial \gamma(\phi)}{\partial \phi} + \lambda_\Omega \frac{\partial R_T}{\partial \phi}. \tag{8}$$

The left-hand side of equation (8) captures the effect of increasing refuge on agricultural productivity. This effect includes a short-run cost since less of the more productive Bt crop is planted, and a long-run benefit since resistance develops more slowly, improving the long-run efficacy of Bt. The right-hand side captures the effect of increasing refuge on pesticide use and resistance. For pesticide use, increasing refuge tends to increase supplemental control in the short run because less of the crop is protected by Bt. In the long run, pesticide use may diminish because resistance develops more slowly and supplemental treatments are reduced. Resistance tends to decline as refuge increases, since selection pressure is reduced. However, if supplemental treatments result on refuge due to more abundant pests, it is possible for resistance to increase.

Model Implementation

The conceptual model demonstrates how measures of agricultural productivity and conventional pesticide use can be incorporated into the current biological framework to assess economic and environmental tradeoffs. Given complex interactions among refuge, treatment thresholds, and pest pressure and resistance, the previous discussion was based largely on intuition. To gain additional insight, more structure is incorporated to develop a simulation model that is flexible enough to customize to a variety of diverse production regions. To maintain a manageable scope, however, focus is devoted to use of Bt corn to control the European corn borer in a region characteristic of the north central United States.

The ECB is a mobile diploid that reproduces sexually, with as many as four generations a year. It causes $1 billion in annual damage and control costs to U.S. farmers (Mason et al.). Southern, warmer climates experience three to four generations, while more temperate northern climates face one to two generations.[5] A bivoltine (two-generation) population is typical for most of the north central U.S. (Mason et al.).

Prior to the 2000 growing season, we are unaware of a confirmed case of resistance to Bt corn in the field. The lack of a confirmed case of resistance provides obstacles to understanding how resistance will evolve. Given a lack of empirical information on

[5] In some areas, farmers can face two different strains of European corn borer. For instance, a farmer may face both a univoltine and a bivoltine population. While not considered here, the model can be readily extended to such scenarios.

resistance, the Hardy-Weinberg model is used to characterize resistance, which is assumed conferred by a single allele that is not sex linked.[6] There are two types of alleles: resistant and susceptible. Each ECB possesses two alleles, one from its mother and one from its father, and can be one of three genotypes: a resistant homozygote (with two resistant alleles), a heterozygote (with one resistant allele), or a susceptible homozygote (with no resistant alleles).

R_g is the proportion of resistant alleles in the ECB population in generation g. The Hardy-Weinberg model implies the proportion of each genotype is

$$\rho^{HW}(R_g) = \left[R_g^2,\ 2R_g(1 - R_g),\ (1 - R_g)^2\right],$$

where the first element of the vector corresponds to resistant homozygotes, the second to heterozygotes, and the third to susceptible homozygotes.

The Hardy-Weinberg model assumes no selection pressure (i.e., the survival rates for all genotypes are equal) and random mating. Bt corn imposes selection pressure on ECB with at least one susceptible allele. Biological models show that the random mating assumption may fail when refuge is poorly configured across the landscape. These models also show that nonrandom mating diminishes the effectiveness of refuge. Therefore, the traditional model is modified for selection and nonrandom mating.

To incorporate selection, let σ_g^i be a 1×3 vector of genotypic survival rates for crop i in generation g. These survival rates depend on natural survival rates and supplemental control:

$$\sigma_g^i = \begin{cases} \sigma^i \nu_g & \text{for } \sigma^i \cdot \rho_g N_g > \tau_g, \\ \sigma^i & \text{otherwise,} \end{cases}$$

where σ^i is a 1×3 vector of natural genotypic survival rates on crop i; and ν_g is the survival rate, τ_g is the economic threshold for supplemental conventional pesticide applications, ρ_g is a 1×3 vector of genotypic proportions, and N_g is the average number of pests per plant in generation g. When $\sigma^i \cdot \rho_g N_g > \tau_g$, the natural survival rate of ECB warrants supplemental control, and so survival rates and production costs are adjusted accordingly.

Nonrandom mating is addressed by assuming a fixed proportion of ECB (κ) do not mate randomly. Surviving ECB fall randomly into one of three mating pools: ECB from refuge, ECB from Bt corn, and ECB from refuge and Bt corn. The proportion falling into each pool depends on refuge, net survival rates, and nonrandom mating. The Hardy-Weinberg model with selection is applied to each pool to determine new genotypic proportions, after which oviposition redistributes ECB uniformly over the region.

With these modifications, the proportion of resistant alleles evolves according to

$$R_{g+1}(R_g, N_g, \phi, \tau) = \frac{\phi\sigma_g^0 \mathbf{M}\rho_g' + (1 - \phi)\sigma_g^1 \mathbf{M}\rho_g'}{\phi\sigma_g^0 \cdot \rho_g + (1 - \phi)\sigma_g^1 \cdot \rho_g},$$

where $\mathbf{M}$ is a 3×3 diagonal matrix with the diagonal equal to [1.0, 0.5, 0.0]. For the population dynamics, genotypic proportions evolve according to

[6] The Hardy-Weinberg model lies at the foundation of population genetics due to its remarkable ability to predict gene frequencies and heritability (see Gould; Onstad and Gould 1998a, b; Roush and Osmond).

$$\rho_{g+1} = (1-\kappa)\rho^{HW}(R_{g+1}) + \kappa \frac{\phi\sigma_g^0 \cdot \rho_g \rho^{HW}(R_{g+1}^0) + (1-\phi)\sigma_g^1 \cdot \rho_g \rho^{HW}(R_{g+1}^1)}{\phi\sigma_g^0 \cdot \rho_g + (1-\phi)\sigma_g^1 \cdot \rho_g},$$

where

$$R_{g+1}^i(R_g) = \frac{\sigma_g^0 \mathbf{M}\rho_g'}{\sigma_g^0 \cdot \rho_g}$$

is the proportion of resistant alleles from nonrandomly mating ECB in crop i.[7]

Most ECB population models focus on within-season development and are inappropriate for the analysis. An exception is Onstad, who develops a temporally explicit bivoltine ECB model for single-season field or multi-season regional analysis. Preliminary simulations using a variety of different population models suggest the most important factor influencing the economic and environmental tradeoffs is whether Bt corn suppresses the ECB. The ECB can recover rapidly from occasional climatic and environmental shocks that suppress populations, but whether it can rapidly recover from the sustained population reductions imposed by Bt corn remains a question.

We utilize a simple population model based on the logistic growth function to demonstrate the sensitivity of the model to suppression:

$$N_{g+1}(R_g, N_g, \phi, \tau) = \beta_{0g} + (1+\beta_{1g})S_g + \beta_{2g}S_g^2,$$

where $S_g = [\phi\sigma_g^0 \cdot \rho_g + (1-\phi)\sigma_g^1 \cdot \rho_g]N_g$ is the average survival rate of pests per plant in generation g; and β_{0g}, β_{1g}, and β_{2g} are parameters for generation g. The parameters β_{1g} and β_{2g} are the intrinsic rate of growth and carrying capacity from a standard logistic growth function. The parameter β_{0g} captures factors limiting suppression and does not appear in a standard logistic growth function.

With $R_{g+1}(R_g, N_g, \phi, \tau)$ and $N_{g+1}(R_g, N_g, \phi, \tau)$, equations (1) and (2) become:

(1′) $$R_{t+1} = R_2\big(R_1(R_t, N_t, \phi, \tau), N_1(R_t, N_t, \phi, \tau), \phi, \tau\big)$$

and

(2′) $$N_{t+1} = N_2\big(R_1(R_t, N_t, \phi, \tau), N_1(R_t, N_t, \phi, \tau), \phi, \tau\big).$$

ECB damage to corn is typically measured conditionally on the degree of tunneling or number of pests per plant. Since the degree of tunneling does not differentiate between first- and second-generation damage, damages are based on pests per plant, which is the unit of measurement used for equation (2′). Mason et al. report an average constant proportion of damage for first- and second-generation ECB; therefore, equation (3) becomes:

(3′) $$D_t^i = \text{Min}\big\{d_1\sigma_1^i \cdot \rho_1 N_t + d_2\sigma_2^i \cdot \rho_2 N_1(R_t, N_t, \phi, \tau), 1.0\big\},$$

where d_1 and d_2 are the average constant proportion of yield loss for first- and second-generation ECB, and $\sigma_g^i \cdot \rho_g$ is the net survival rate of ECB on crop i. Equation (3′) also restricts the proportion of damages to not exceed 1.0.

Having parametrically specified resistance, the population dynamics, and damages, benchmark parameters are chosen. Table 1 presents the benchmark configuration for

[7] A more detailed explanation of the derivation of these equations can be found in Hurley et al.

Table 1. Benchmark Parameter Values

Parameter Description	Initial Value
ECONOMIC:	
Planning horizon (years)	15
Interest rate	0.04
Price of corn ($/bushel)	$2.35
Pest-free yield (bushels/acre)	130
Production cost ($/acre)	$185.00
Cost of conventional pesticide applications ($/acre)	$14.00
1st generation constant marginal yield loss (pests/plant)	0.055
2nd generation constant marginal yield loss (pests/plant)	0.028
1st generation economic threshold (pests/plant)	1.04
2nd generation economic threshold (pests/plant)	2.44
BIOLOGICAL:	
Number of generations	2
Refuge survival rates	1.00
Survival rate of resistant homozygotes on Bt corn	1.00
Survival rate of susceptible homozygotes on Bt corn	0.00
Survival rate of heterozygotes on Bt corn	0.02
1st generation survival rate for conventional pesticide application	0.20
2nd generation survival rate for conventional pesticide application	0.33
Proportion of nonrandom mating	0.0
Initial pest population (pests/plant)	0.23
Initial frequency of resistant alleles	3.2×10^{-4}

all but the population dynamics. Table 2 presents estimated parameters for two alternative population models.

National Agricultural Statistics Service (NASS) and Economic Research Service (ERS) data provide values for the real price, pest-free yield, and production cost of refuge corn. The real price of corn ($2.35) is the monthly average from 1991 through 1996 deflated to 1992.[8] The average Iowa yield from 1991–96 was about 123 bushels per acre. Assuming an average annual ECB yield loss of 6.4% (Calvin) implies the pest-free yield is 130 bushels per acre. Excluding returns to management, the average production cost ($185) comes from 1995 ERS corn budgets deflated to 1992 prices. The interest rate is 4%.

The pest-free yield and production cost of Bt corn is the same as refuge for the benchmark simulation. While farmers typically pay a $7 to $10 per acre technology fee for Bt seed, this premium does not reflect an increase in the marginal cost of growing Bt corn. The difference in the marginal production cost between Bt and non-Bt seed is the result of more rigorous quality control for Bt seed (personal communication with Paula Davis, Monsanto Corp.). Initially assuming the differences in production costs are negligible focuses attention on the resistance management benefits of refuge.

[8] Depending on the rate of adoption of Bt corn, there could be supply-side price effects that are not treated and depend on refuge size.

Table 2. Maximum-Likelihood Estimates for European Corn Borer Population Models

	FIRST GENERATION		SECOND GENERATION	
Description	*Heavy* Suppression	*Light* Suppression	*Heavy* Suppression	*Light* Suppression
Constant	—	0.028 (0.61)	—	0.26 (0.82)
Previous generation's population	-0.757*** (21.64)	-0.802*** (11.74)	7.76*** (4.48)	5.96** (2.24)
Previous generation's population squared	-0.053*** (3.71)	-0.040* (1.93)	-10.30** (2.35)	-8.13* (1.67)
Maximized log-likelihood function	34.08	34.48	-61.90	-61.13
$\chi^2_{[1]}$ test of model 1 versus model 2	0.80		1.54	
No. of observations	43		49	
Equilibrium population without Bt corn (pests/plant)	0.248	0.227	1.54	1.43
Calibration factor[a]	1.01	—	0.97	—

Notes: Single, double, and triple asterisks (*) denote significance at the 10%, 5%, and 1% levels of confidence, respectively. Numbers in parentheses are the absolute values of the *t*-statistics.

[a] Calibration factors are used to calibrate the equilibrium populations without Bt corn in order for model 1 to equal model 2.

There is more uncertainty regarding genotypic survival rates, the resistant allele frequency, and the degree of nonrandom mating. Consistent with Gould, random mating is initially assumed, and the survival rate of all genotypes on refuge and resistant homozygotes on Bt corn are normalized to 1.0. Gould also assumes the frequency of resistant alleles is 1.0×10^{-3} based on tobacco budworm data, and that the survival rate of susceptible homozygotes and heterozygotes on Bt corn is positive. The relative survival rate of 0.1 implied by these assumptions is contrary to recent field surveys. For example, Pierce, Weinzierl, and Steffey found a relative survival rate of 4.0×10^{-7}. The low observed survival rate of ECB on Bt corn suggests no susceptible homozygotes survive. If this is the case, Hurley et al. estimate the heterozygote survival rate to be 0.02 and the fre-quency of resistant alleles to be 3.2×10^{-4} using 1997 field data. These estimates are adopted for the benchmark since they imply a relative survival rate of 4.1×10^{-5}, which is more consistent with recent field observations.

Population parameters for two models are obtained using maximum-likelihood techniques and the 1960s ECB population data reported in Calvin. The first model assumes $\beta_{0g} = 0$, or that *Heavy* suppression occurs. The second assumes $\beta_{0g} \neq 0$, or that suppression is *Light*. The results of these estimations are reported in table 2. The hypothesis that $\beta_{0g} = 0$ for both generations is not rejected, which supports *Heavy* suppression. However, both models are explored since there is skepticism about the ability of Bt corn to result in *Heavy* suppression. For *Heavy* suppression, the uncontrolled equilibrium populations for the first and second generations are 0.25 and 1.5 pests/plant, respectively. For *Light* suppression, the uncontrolled equilibrium populations are 0.23 and 1.4. Therefore, the *Heavy* suppression model is calibrated using the multiplicative factors reported in table 2 for greater comparability.

The constant marginal damage rates for first- and second-generation ECB (0.055 and 0.028) are obtained from Ostlie, Hutchison, and Hellmich (refer to table 1). Combined with the equilibrium populations, the implied average annual yield loss is 5.3%, which is 20% lower than the 6.4% reported in Calvin. The cost of a supplemental conventional pesticide treatment for the first and second generations ($14 per acre) is from Mason et al., as are the survival rates for these treatments (0.20 and 0.33). The first- and second-generation economic thresholds (1.04 and 2.44 pests per plant) are calculated based on Mason et al. using the benchmark price, pest-free yield, and marginal damages. Note that these economic thresholds will never trigger supplemental treatments in the benchmark simulation but, as Demetra et al. indicate, conventional pesticide treatments for ECB in the north central U.S. are indeed rare due to high costs and poor efficacy. Production costs are assumed to include scouting.[9]

The final parameter to specify is the length of the planning horizon for assessing the benefits and costs of resistance management. A 15-year planning horizon is used to conform to the assumptions made by the ILSI/HESI and Demetra et al.

Simulation Results

Intuition suggests refuge reduces short-run productivity and increases short-run conventional pesticide use by reducing the percentage of acreage protected by Bt corn. Refuge also bolsters long-run productivity and decreases long-run pesticide use by preserving the efficacy of Bt. Increasing refuge would appear to reduce resistance and improve the long-run efficacy of Bt. Within the context of the general model, however, it is possible for an increase in refuge to increase resistance and decrease the long-run efficacy of Bt by increasing supplemental treatments on refuge. A better understanding of these complex interactions and important economic and environmental tradeoffs is obtained by exploring the benchmark simulation and its sensitivity to changes in various model parameters.

Figure 1 illustrates the tradeoff between the short- and long-run benefits of refuge by showing the annualized net present value of agricultural production and the final proportion of resistant alleles as refuge increases from 0 to 100% for *Heavy* and *Light* suppression. Conventional pesticide use does not affect this figure because it is never warranted in the benchmark simulation.

The final proportion of resistant alleles is the same with either *Heavy* or *Light* suppression because the development of resistance depends on the relative survival rates, which are the same when supplemental treatments are unwarranted. Increasing refuge from 0 to 10% has little effect on resistance. As the percentage of refuge increases from 10% to 20%, resistance decreases rapidly. Increasing refuge above 20% continues to decrease resistance, though modestly because it is already so low.

Production value initially increases, but then declines as refuge increases from 0 to 100%. With *Heavy* suppression, production value declines almost immediately. With *Light* suppression, production declines once refuge exceeds 10.6%. When the production value starts to decline, the decline is initially more rapid when suppression is *Light*. As refuge approaches 100%, the decline is more rapid when suppression is *Heavy*. Also note

[9] While scouting Bt corn is typically not necessary, it is recommended to monitor for resistance.

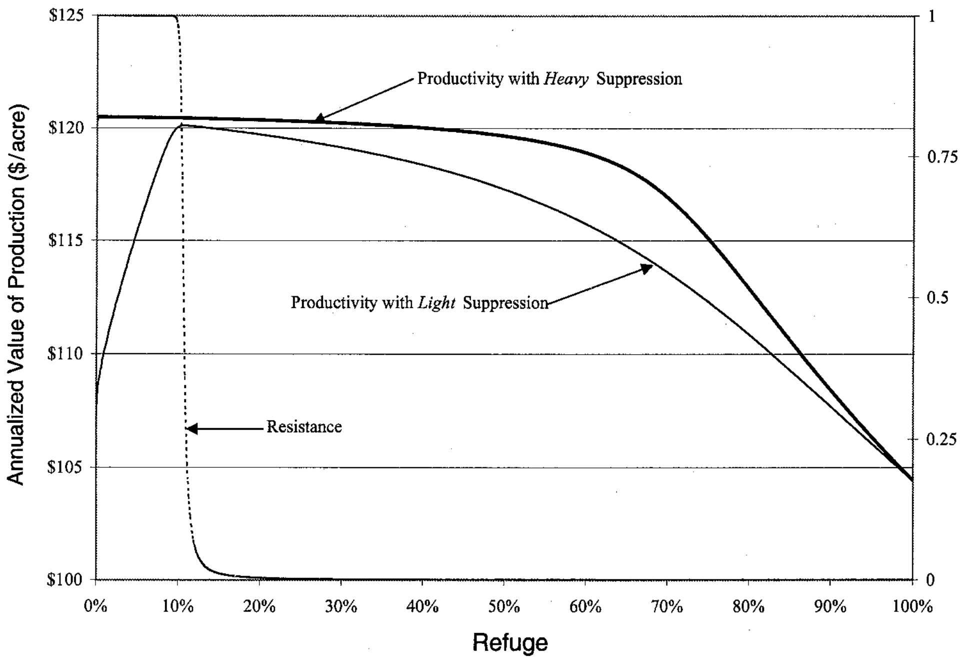

Figure 1. Tradeoff between the final proportion of resistant alleles and the annualized value of agricultural production for *Heavy* and *Light* suppression

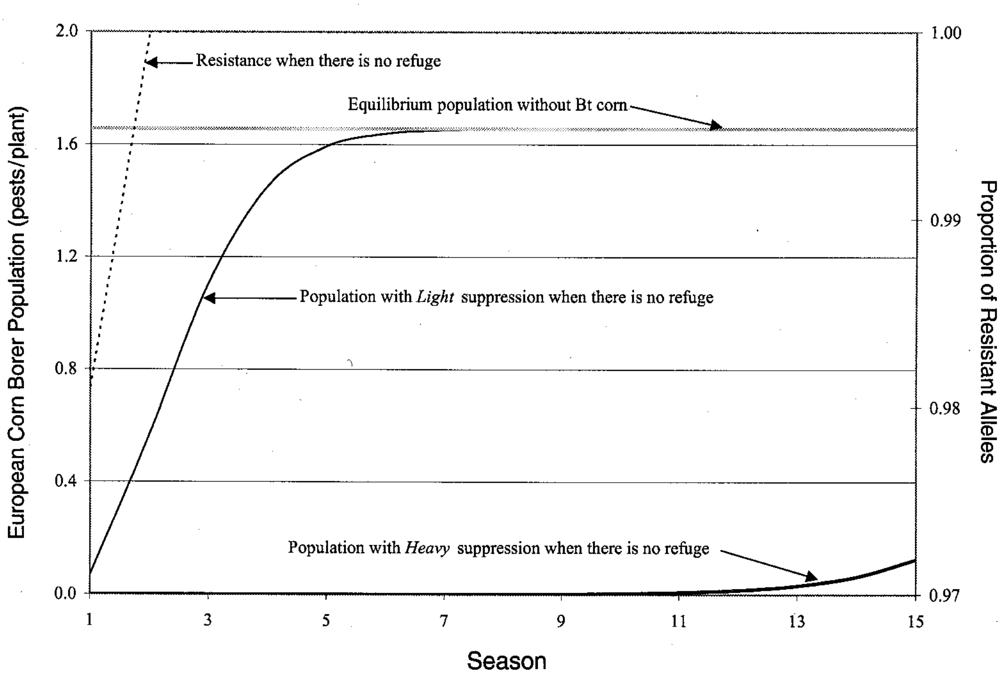

Figure 2. Evolution of the pest population and resistance for both *Heavy* and *Light* suppression when no refuge is planted

that production value is higher when suppression is *Heavy* because there is better overall ECB control. These results are qualitatively similar for all parameterizations explored.

To better understand the results in figure 1, it is instructive to consider how Bt corn and the development of resistance influence ECB populations over time. Figure 2 tracks resistance and ECB pressure for both *Heavy* and *Light* suppression when no refuge is planted. With no refuge, resistance develops rapidly. Before resistance develops, the universal planting of Bt corn decimates ECB populations regardless of suppression. After resistance develops, a rapid population resurgence occurs when suppression is *Light*. Within eight seasons, the population rebounds to initial levels. Alternatively, when suppression is *Heavy*, the population does not begin to recover until the ninth season, and by the end of the 15th season the population is still less than 10% of its original level.

Refuge moderates the initial decline in ECB, but extends the efficacy of Bt corn allowing better control in later seasons. The benefits of increasing refuge are limited when there is enough refuge to provide effective control throughout the planning horizon. Increasing refuge beyond this point serves only to increase ECB pressure. With *Light* suppression, better control later provides substantial benefits by mitigating resurgent populations. With *Heavy* suppression, better control later provides few benefits because the ECB is nearly eradicated and recovers slowly. Moderating this near eradication with more refuge lowers the value of production because it is easier for the ECB to reestablish.

Planting some refuge benefits production over the long run, but too much refuge can be detrimental. If maximizing the long-run value of production is the EPA's only objective, less than 1% refuge is reasonable with *Heavy* suppression, while about 10.6% refuge is reasonable with *Light* suppression. With less than 1% refuge and *Heavy* suppression, final resistance is essentially 1.0, and production is valued at $120.50 as compared to $104.44 per acre when no Bt corn is planted. With 10.6% refuge and *Light* suppression, the proportion of final resistance is 0.52, and production value is $120.13 as compared to $104.44 per acre.

The EPA states that it is in the public's interest to preserve the efficacy of Bt as a reduced-risk pesticide by managing resistance (U.S. EPA). Therefore, the value of production is not the EPA's sole objective for resistance management. The agency is also concerned with conventional pesticide use, the impact of resistance on the effectiveness of Bt foliar sprays commonly used by organic producers, and other benefits that are external to corn producers. Determining the public value of these other benefits is beyond the scope of this analysis. However, the model can be used to generate the marginal and average costs of resistance management which, when combined with estimates of the other benefits, determine how much refuge should be planted.

The Lagrangian multiplier λ_Ω captures the marginal cost of increasing refuge to manage resistance in terms of decreased production. When the constraint for conventional pesticide use does not bind,

$$\lambda_\Omega = \left. \frac{\partial \Pi(\phi)}{\partial R_T} \right|_{\phi=\phi^*},$$

where ϕ^* is the constrained optimum. The average cost of resistance management is written as:

$$\frac{\Pi(\phi)|_{\phi=\phi^*} - \Pi(\phi)|_{\phi=\phi^{**}}}{R_T|_{\phi=\phi^*} - R_T|_{\phi=\phi^{**}}},$$

where ϕ^{**} is the proportion of refuge that maximizes production without constraints on resistance or conventional pesticide use.

Figures 3(a) and 3(b) show the marginal and average costs of increasing susceptibility at the end of the planning horizon for *Heavy* and *Light* suppression, respectively. When susceptibility is below what is necessary to maximize the value of production (below 0.58 with *Light* suppression), the cost of resistance management (increasing susceptibility) is zero. When refuge is above what is necessary to maximize production, the cost of resistance management is positive.

Average and marginal costs with *Heavy* suppression are nonmonotonic. Costs of increasing susceptibility above zero are initially quite high because it requires a significant increase in refuge acreage above what is necessary to maximize production. Costs fall dramatically for further increases because the response of susceptibility to increases in refuge is large (see figure 1). Finally, the marginal cost rises significantly as susceptibility increases above 0.9. The shapes of the cost curves in figure 3(a) are indicative of large fixed costs and small marginal costs: startup costs are large, but operating costs are quite small.

The *Light* suppression cost curves are shown in figure 3(b). Because the production-maximizing refuge level is approximately 10%, and the ending susceptibility level is less than 1.0, increasing susceptibility further is accomplished by increasing refuge acres a small amount. That is, there is no large "fixed cost" to increasing susceptibility. Within the context of resistance management, this implies that when suppression is *Light*, the greater the external benefits of resistance management, the more refuge should be planted. When suppression is *Heavy*, the external benefits of resistance management must be substantial before increasing refuge can be justified. However, once increasing refuge is justified, typically more refuge should be planted than if suppression is *Light*.

Sensitivity Analysis

Previous biological models focus on the sensitivity of resistance developing to the initial frequency of resistant alleles, nonrandom mating, and the heterozygote survival rate due to uncertainty regarding these parameters. In addition to exploring the sensitivity of the model's results to these biological factors, changes in the planning horizon, interest rate, price of corn, pest-free yield, marginal production cost of Bt corn, spray application cost, and marginal damages are also considered.

A summary of the sensitivity analysis is reported in table 3, where the parameter range of the sensitivity analysis is reported in column 1 as (minimum value, maximum value). The unconstrained percentage of refuge (column 2) that maximizes the value of production is also reported with production, resistance, and pesticide use.[10] In columns 2–5 of table 3, values are reported as {(minimum value with *Heavy* suppression, maximum value with *Heavy* suppression); (minimum value with *Light* suppression, maximum value with *Light* suppression)}.[11]

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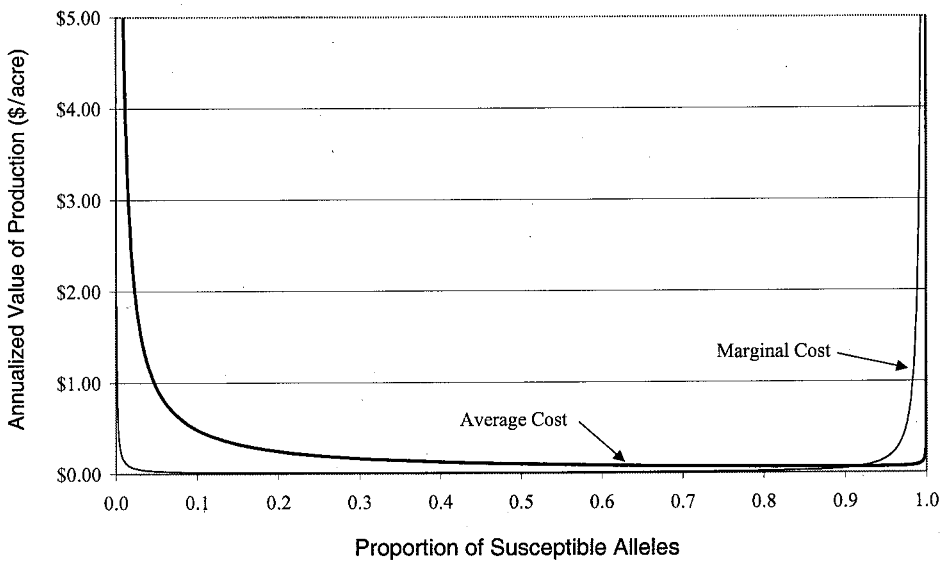
[10] Results from a similar sensitivity analysis that constrained the final proportion of resistant alleles to less than 0.01 are available from the authors upon request.

[11] Minimum and maximum values may not correspond directly to the minimum and maximum values of the parameters.

PANEL (a): *Heavy* Suppression



PANEL (b): *Light* Suppression

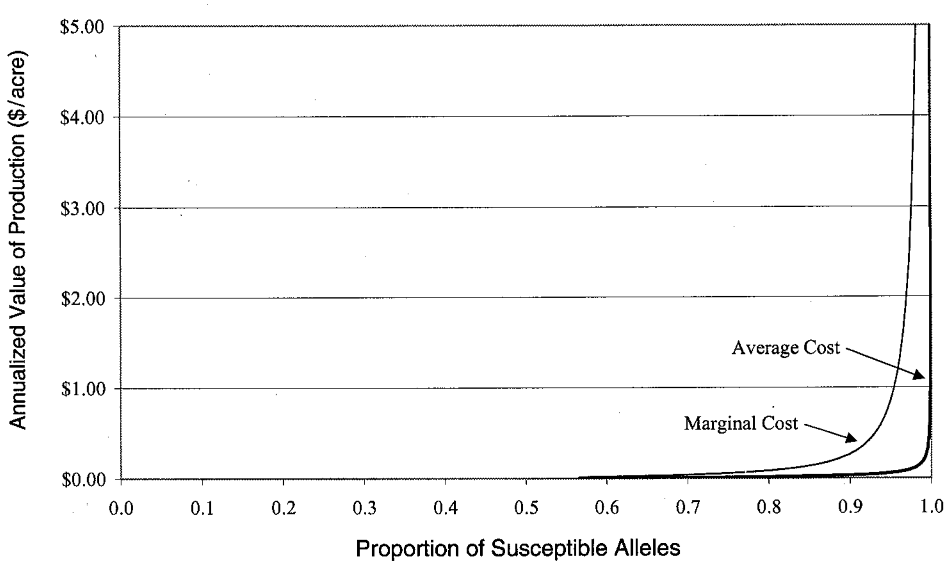


Figure 3. Marginal and average costs of increasing susceptibility from 0 to 1.0 for (a) *Heavy* and (b) *Light* suppression

Table 3. Summary of Sensitivity Analysis for the Optimum Without Constraints on Resistance or Pesticide Use

Description	[1] Parameter Value[a] (min, max)	[2] Unconstrained Refuge[b] (%)	[3] Production[b] (annualized $/acre)	[4] Resistance[b] (proportion of resistant alleles)	[5] Pesticide Use[b] (average annual applications)
Planning horizon	(5, 25)	{(0.0, 0.8); (2.8, 17.3)}	{(120.50, 120.50); (119.86, 120.39)}	{(1.00, 1.00); (0.42, 0.68)}	{(0.0, 0.0); (0.0, 0.0)}
Interest rate	(0.00, 0.25)	{(0.1, 0.2); (10.0, 10.6)}	{(120.50, 120.50); (120.09, 120.13)}	{(1.00, 1.00); (0.48, 0.95)}	{(0.0, 0.0); (0.0, 0.0)}
Price of corn	($1.70, $3.50)	{(0.2, 0.2); (10.6, 10.6)}	{(36.00, 270.00); (35.73, 269.44)}	{(1.00, 1.00); (0.55, 0.55)}	{(0.0, 0.0); (0.0, 0.0)}
Pest-free yield	(100, 200)	{(0.2, 0.2); (10.6, 10.6)}	{(50.00, 285.00); (49.71, 284.42)}	{(1.00, 1.00); (0.55, 0.55)}	{(0.0, 0.0); (0.0, 0.0)}
Proportion decrease in Bt corn pest-free yield	(0.00, 0.25)	{(0.2, 100.0); (10.6, 100.0)}	{(104.18, 120.50); (104.44, 120.13)}	{(0.00, 1.00); (0.00, 0.55)}	{(0.0, 0.0); (0.0, 0.0)}
Marginal production cost of Bt corn	($0.00, $10.00)	{(0.2, 58.7); (10.6, 42.7)}	{(114.92, 120.50); (112.38, 120.13)}	{(0.00, 1.00); (0.00, 0.55)}	{(0.0, 0.0); (0.0, 0.0)}
Spray application cost	($0.25, $14.00)	{(0.2, 0.5); (10.6, 31.5)}	{(120.50, 120.50); (119.86, 120.13)}	{(1.00, 1.00); (0.53, 0.71)}	{(0.0, 0.0); (0.0, 0.67)}
Proportion of benchmark constant marginal damages	(0.50, 2.00)	{(0.2, 0.2); (10.6, 10.6)}	{(120.50, 120.50); (119.75, 120.31)}	{(1.00, 1.00); (0.55, 0.55)}	{(0.0, 0.0); (0.0, 0.0)}
Heterozygote survival rate	(0.00, 1.00)	{(0.0, 33.6); (0.8, 66.5)}	{(117.10, 120.50); (111.95, 120.48)}	{(0.97, 1.00); (0.31, 0.79)}	{(0.0, 0.0); (0.0, 0.0)}
Proportion of nonrandom mating	(0.00, 0.50)	{(0.2, 2.8); (10.6, 29.0)}	{(120.48, 120.50); (119.18, 120.13)}	{(1.00, 1.00); (0.49, 0.55)}	{(0.0, 0.0); (0.0, 0.0)}
Initial resistance frequency	(1.0×10^{-6}, 1.0×10^{-3})	{(0.0, 0.5); (4.4, 13.9)}	{(120.50, 120.50); (119.98, 120.36)}	{(1.00, 1.00); (0.43, 0.60)}	{(0.0, 0.0); (0.0, 0.0)}

[a] Range of parameter values for sensitivity analysis: (minimum value, maximum value).

[b] Resultant range of values from the sensitivity analysis: {(minimum value with *Heavy* suppression, maximum value with *Heavy* suppression); (minimum value with *Light* suppression, maximum value with *Light* suppression)}. These values may not correspond directly to the minimum and maximum parameter values.

More refuge is necessary to maintain the efficacy of Bt corn when the planning horizon lengthens. As the planning horizon increases from 5 to 25 years, the unconstrained percentage of refuge increases from 0.0 to 0.8 for *Heavy* and from 2.8 to 17.3 for *Light* suppression. Production is constant at $120.50 per acre for *Heavy* and decreases from $120.39 to $119.86 per acre for *Light* suppression. Resistance with unconstrained refuge is always 1.0 for *Heavy* suppression because it is optimal to exhaust susceptibility while nearly eradicating the ECB. For *Light* suppression, final resistance increases from 0.42 to 0.68. Pesticide use is unaffected because supplemental treatments are not economical.

Increasing the interest rate lowers the benefits of resistance management by lowering the value of future production. As the interest rate increases, the unconstrained refuge falls for *Heavy* and *Light* suppression. Increasing the price of corn or pest-free yield, or decreasing marginal ECB damages, serves to boost revenues relative to production costs, which has virtually no effect on refuge and resistance for either *Heavy* or *Light* suppression. Production value with the unconstrained refuge increases. As the pest-free yield of Bt corn decreases, or the marginal cost of Bt corn increases, Bt corn becomes less valuable relative to refuge. This serves to increase refuge and decrease the production value and resistance for *Heavy* and *Light* suppression. Supplemental pesticide use remains uneconomical over these ranges of parameter values.

Decreasing the application cost of conventional pesticides reduces economic thresholds and increases supplemental treatments. Refuge increases for both *Heavy* and *Light* suppression, though more so with *Light* suppression since pesticide applications are more frequent. Resistance for *Heavy* suppression is constant at 1.0 because near eradication is still optimal. Production value and resistance for *Light* suppression and production value for *Heavy* suppression are erratic due to the discrete nature of the treatment threshold. When application costs fall, increasing refuge to preserve susceptibility is less costly in terms of production value because there is a cheap substitute available for supplemental control. However, preserving susceptibility is more costly in terms of increased pesticide use.

The average proportion of resistant alleles in the surviving ECB population initially increases, but then decreases as the heterozygote survival rate increases. Therefore, increasing the heterozygote survival rate initially encourages, but then discourages resistance. As the heterozygote survival rate increases, refuge initially increases before eventually decreasing for *Heavy* and *Light* suppression. Production value decreases as the ECB becomes harder to control. With *Heavy* suppression, resistance eventually decreases because surviving heterozygotes contribute to susceptibility even with near eradication. With *Light* suppression, an increase in resistance is followed by a decrease. Refuge increases for both *Heavy* and *Light* suppression. Supplemental treatments are not economical.

As nonrandom mating increases, the development of resistance is more rapid because resistant homozygotes are more likely to mate with each other. Therefore, refuge for both *Heavy* and *Light* suppression increases, while production value falls. Resistance is constant at 1.0 for *Heavy* suppression and decreases before increasing for *Light* suppression. Supplemental treatments are never economical.

Increasing the initial frequency of resistant alleles increases the unconstrained and constrained refuge, while decreasing production regardless of suppression. Resistance remains at 1.0 for *Heavy* suppression and increases for *Light* suppression. Supplemental treatments are unwarranted.

Conclusions

Four results emerge from our extension of the current biological framework used to evaluate refuge recommendations to include the tradeoffs associated with measures of agricultural productivity, conventional pesticide use, and resistance when Bt corn is planted to control the European corn borer in the north central United States.

- First, planting refuge acreage not only reduces resistance, but also improves long-run agricultural productivity. Refuge benefits long-run agricultural productivity by maintaining the efficacy of Bt and providing better control of the pest over a longer period.

- Second, the productivity benefits of resistance management as well as the costs are extremely sensitive to population dynamics. The high efficacy of Bt crops decimates the pest. If the pest rebounds rapidly, refuge enhances long-run productivity by allowing better control of resurgent populations. However, if the pest struggles to recover due to near eradication, refuge provides little productivity enhancement because there are so few pests left to control. As a result, there are relatively low fixed and high marginal costs to increasing refuge to slow resistance with a resurgent pest. When the pest struggles to recover, there are relatively high fixed and low marginal costs to increasing refuge to slow resistance. Therefore, it is harder for the EPA to justify increasing refuge to manage resistance when the pest struggles to recover. However, if resistance management is justified, then more refuge should be planted than with a resurgent pest.

- Third, the average cost of increasing refuge to maintain resistance below 0.01 is low, usually less than 1% of the value of agricultural production. This result suggests that increasing refuge for resistance management is inexpensive. However, the marginal cost of increasing refuge is more substantial and increases rapidly once there is sufficient refuge to preserve the efficacy of Bt. Therefore, even if the average cost is low, the high marginal cost can make increasing refuge to slow resistance inappropriate.

- Fourth, more refuge is needed for resistance management when conventional spray applications are economical on refuge. The marginal and average costs of increasing refuge to slow resistance in terms of agricultural production are lower because there is a cost-effective alternative to Bt crops. However, the marginal and average costs in terms of conventional pesticide use increase with the substitution of conventional spray applications for Bt crops.

These results demonstrate the importance of considering both the economic and environmental tradeoffs inherent in resistance management. Much more work is needed to provide policy makers with reliable tools for assessing the benefits and costs of resistance management. This investigation's focus on a constant refuge can be viewed as a second-best strategy. How temporal variations in refuge can further increase agricultural productivity and decrease conventional pesticide use and resistance remains to be explored. The full adoption and compliance scenario presented here is unlikely to be met in practice. If adoption is less than full, the model will tend to overestimate the benefits of refuge, while underestimating the costs. Alternatively, if compliance with refuge requirements is less than full, the model will tend to underestimate the benefits of refuge, while overestimating the costs. Behavioral models of grower adoption and compliance behavior remain to be developed and incorporated into current modeling efforts. Future efforts would also benefit from a more explicit treatment of parameter uncertainty and stochastic population dynamics.

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